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INFLUENCE OF VARIOUS TYPES OF LIGHT ON GROWTH AND PHYSICOCHEMICAL COMPOSITION OF BLUEBERRY (*Vaccinium corymbosum* L.) LEAVES

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ABSTRACT

It is important to use light that has a positive effect on plants. For plant growers, achieving the lowest possible cost of shrub production is crucial. We investigated the influence of light (white and violet LEDs as well as fluorescent white and red light) on the rooting and growth of blueberry cuttings (*V. corymbosum* L.) 'Aurora' and 'Huron'. Blueberry cuttings (4 cm tall) were planted into boxes with peat, which were placed in a phytotron at 22°C and illuminated for 16 hours a day. The plants died under the red fluorescent light source and, therefore, we discontinued its use. The other three light sources had a positive effect on plant growth and development. The light source had little effect on the content of macroelements in the leaves. Plants grown under white fluorescent and white LED light did not significantly differ in the height (22.0–25.8 cm), proline (4.67–7.23 μmol g^{-1}), and polyphenol content (4987–5212 mg 100 g^{-1}). In both cultivars, the violet LED light reduced plant growth and increased the content of polyphenols (6,448 mg 100 g^{-1}) and proline (8.11–9.06 μmol g^{-1}) in the leaves, which may indicate abiotic stress.
During the rooting of highbush blueberry cuttings, it is advisable to use white LED light. It has a positive economic impact on crop production due to low electricity consumption and it benefits the environment by eliminating mercury. The plant quality is similar to that of fluorescent white light.

Key words: phytotron, LED light, polyphenols, proline, macro- and microelements

INTRODUCTION

The genus *Vaccinium*, which belongs to the family Ericaceae, comprises approximately 400 species. The largest producers of blueberry are the USA, Chile, and Canada [Brazelton and Young 2017]. In Europe, blueberry production is concentrated in Poland, Germany, and Spain [Brazelton 2013]. In recent years, there has been an increasing consumer interest in blueberry fruit mainly because of its taste and health-promoting properties. The average annual growth rate of blueberry production worldwide is 8.2% (FAO UN 2018). Despite the increase in blueberry cultivation, the selling price of blueberries still remains very high [Podymniak 2015].

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Also the leaves are a very valuable material besides the fruit. Blueberry leaves, prepared and consumed as tea, are a rich source of potent phenolic antioxidants, and have very high TP content and significant reducing capacity according to the FRAP assay [Piljac-Žegarac et al. 2009]. Blueberry leaf tea supports digestion and is especially useful after eating fatty and hard to digest foods. This tea also has blood glucose lowering properties, hence it is recommended in the early stages of diabetes. It is also used in inflammatory conditions of the urinary and digestive systems. The infusion is aromatic and has a bitter, tannic taste due to the high amount of polyphenols [Wang et al. 2015].

Light is the primary environmental factor stimulating plant growth and development [Bourget 2008, Massa et al. 2008, Morrow 2008, Hogewoning et al. 2010], and its control is an increasingly used tool in production [Zoratti et al. 2014, Demotes-Mainard et al. 2016]. The intensity and composition of the radiation reaching the plants has a very strong influence on the formation of the aboveground plant parts and is a key factor in morphological development and leaf formation of plants [Pilarski and Kocurek 2014]. Plants detect and react to changes in light wavelengths with different types of photoreceptors, including phytochromes, thereby modulating their growth and development [Kami et al. 2010, Burgie et al. 2014, Galvão and Fankhauser 2015, Demotes-Mainard et al. 2016]. Phytochromes can be inactive or active, and the balance between these two forms changes dynamically with changes in the light spectrum composition in the range 300–800 nm, and it is strongly correlated with the red/far red (R/FR) ratio similar as for blue light [Holmes and Smith 1977, Sager et al. 1988, Kong et al. 2018]. For years, the most commonly used light sources for *in vitro* plant cultivation were high-pressure sodium lamps, incandescent lamps, fluorescent, and metal halide lamps [Hahn et al. 2000, Kim et al. 2005, Gupta and Jatothu 2013]; the wavelength of these light sources may not always be appropriate for plants, thereby adversely affecting plant growth and increasing production costs [Kim et al. 2005]. In recent years, light-emitting diodes (LEDs) have increasingly been used as a light source for plants in limited space cultivation [Morrow 2008, Hogewoning et al. 2010, Mengxi et al. 2010, Gupta and Jatothu 2013]. LEDs have found their application because of their good cost efficiency, relatively high power to light conversion rate, different colors (spectrum), relatively low surface temperature, long life, gas-free semiconductor construction, etc. [Bourget 2008, Morrow 2008, Olle and Viršile 2013, Kozai 2016]. Of the various narrow-spectrum lights, the blue and red LEDs are most commonly used for plant growth. The wavelengths of blue and red LED lights (460 and 660 nm, respectively) are highly effective in absorbing chlorophyll, resulting in optimal photosynthetic performance of plants [Massa et.al. 2008, Johkan et.al. 2010, Gupta and Jatothu 2013]. The results of numerous experiments have shown a variable response of plants to LED light, depending on the species and *in vitro* conditions [Hahn et al. 2000, Głowacka 2002, Kurilčik et al. 2008, Hung et.al. 2016].

Phenolic compounds can protect organisms from oxidative stress caused by free radicals [Scalbert et al. 2005]. The antioxidant activity of plant extracts is related to the presence of phytochemicals such as anthocyanins, phenolic acids, flavonoids, and tannins, which increase in stressful situations [Cao et al. 1996, Ochmian et al. 2015]. In addition to glycine betaine (GB), proline is one of the main organic osmolites that accumulate in plants in response to environmental stress, such as drought, salinity, extreme temperatures, UV radiation, and heavy metals [Rzepka-Plevneš et al. 2009, Ashrafa and Foolad 2016, Krupa-Małkiewicz et al. 2018]. Excessive proline accumulation is a common physiological reaction of plants under biotic and abiotic stress conditions [Verbruggen and Hermans 2008, Shevyakova et al. 2009, Liang et al. 2013, Krupa-Małkiewicz et al. 2018].

The aim of the experiment was to study the effect of different types of light on the growth and physico-chemical parameters of blueberry cuttings of Aurora and Huron cultivars.

MATERIALS AND METHODS

Study area and plant material

The experiment was carried out in a commodity farm that produces highbush blueberry plantlets in Dobrzany Municipality (Zachodniopomorskie Voivodeship, Poland) and in the lab of the Department of Plant Genetics, Breeding and Biotechnology, West Pomeranian University of Technology, Szczecin, Poland.

Shoot cultures were incubated in a growth chamber for 5 months at 22°C under four light sources with a 16 h photoperiod and photosynthetic photon flux density (PPFD) uniformly maintained at around 50–60 µmol s^{-1} m^{-2}. The research material included Aurora and Huron cultivars of highbush blueberry (*Vaccinium corymbosum* L.).

Characteristics of the light sources

In the experiment, the following linear LED lamps were used:

1) T8 4 ft (1212 mm) LED tube cool white, 18 W, Toshiba (hereafter referred to as white LED), wavelength 410–780 nm, light at 52 µmol s^{-1} m^{-2} photosynthetic photon flux density (PPFD);

2) T8 Flora LED light source for plants (1200 mm), 18 W, pink color, Greenie (hereafter referred to as violet LED), wavelength 410–510 and 580–710 nm, light at 60 µmol s^{-1} m^{-2} PPFD;

as well as the following linear fluorescent lamps:

3) mercury lamp with a luminophore L 36W/84 T8 Cool White, Lightech (hereafter referred to as white fluorescent lamp), wavelength 400–500, 530–550, and 580–630 nm, light at 36 µmol s^{-1} m^{-2} PPFD;

4) mercury lamp with TLD luminophore 36W/16, RED, Philips (hereafter referred to as red fluorescent lamp), wavelength 600–700 nm, light at 13 µmol s^{-1} m^{-2} PPFD.

Characteristics of the cultivars

'Aurora' (U.S. Plant Patent 15,185). Bushes have moderate vigor, are stocky, and with a spreading growth habit, especially when young. It begins to yield fruit at the end of July and continues to yield until the first days of September [Strik et al. 2014].

Berries are medium to large sized (1.5–2.5 g), dark blue, firm, with a small scar, mild flavored.he fruit needs to be let to hang on the plant to fully ripen and sweeten, and it hangs for much longer time, without shriveling, than Elliott cultivar does.

'Huron' (U.S. Plant Patent 21,777). The plants of this cultivar are vigorous and upright. Canes are numerous and moderately branched, and the fruits are well exposed. Yield is medium (performs better with cross-pollination) [Strik et al. 2014]. Plants possess excellent winter hardiness, and late flowering.

Its berries are moderately large (1.7–2.5 g), with small, dry picking scars, medium blue colored, with excellent firmness and superior flavor if allowed to fully ripen [Hancock 2011].

It is a productive, early ripening cultivar with very high fresh market quality and a long storage life.

Cuttings and substrate characteristics

Shoots were taken from mother plants that grew in the phytotron. The cuttings were cut into 3 cm fragments with two internodes (3 leaves). The first leaf has been removed. The prepared material was planted into boxes measuring 35 cm × 25 cm × 7 cm, and substrate height was 5 cm. In each box, there were 2 × 25 plantlets of a given cultivar arranged in five rows of five plantlets (Fig. 1). Four boxes were prepared for each combination. One repetition consisted of 25 plants. The substrate used in the experiment was a mixture 20 mL of Previcur Energy 840 SL (systemic multi-site fungicide), 20 L water and 90 L peat. Peat had 66.9% organic matter, EC 0.24 mS/cm, volume weight 0.35 kg dm^{-1}, full water capacity 85.2 %vv and pH in KCl 3.44. It was characterized by optimal content for blueberry [Komosa 2007] $N\text{-}NO_3$ + $N\text{-}NO_4$ – 2.64 mg 100 g^{-1}, P – 3.3 mg 100 g^{-1}, K – 5.1 mg 100 g^{-1}, high Ca 38.9 mg 100 g^{-1} and Mg – 7.0 mg 100 g^{-1}.

Measurements and observations

Leaf sampling. For analyses, 2 leaves were collected after 8 weeks from the middle part of all shoots from 20 plants from each box. All measurements (leaf area and colour) and analyses (proline, phenolic and mineral contents) were performed on these leaves. All chemical determinations were performed in triplicate.

Plant size. Plant height was measured four times at monthly intervals using a measuring tape with an accuracy of 1 mm. At the end of the experiment (after 5 months), the leaves were taken and stored for further analyses. On a representative sample of 100 leaves, the area of each leaf was measured with a DIAS 4 scanner (DIAS Infrared GmbH, Germany) [Ochmian et al. 2012].

Color measurement. Color parameters by model Commission Internationale de l'Eclairage (CIE) were: L^* (L^* = 100 indicated white; L^* = 0 indicated black), a^* (+a^* indicated redness; −a^* indicated greenness), and b^* (+b^* indicated yellow; −b^* indicated blue). Color coordinates were determined in the CIE $L^*a^*b^*$ space for the 10° standard observer and the D 65

Fig. 1. Blueberry cuttings

standard illuminant. CIE *L*a*b** was measured was measured using the CM700d spectrophotometer on a representative sample of 100 leaves from each combination (Konica Minolta, Osaka, Japan) [Hunterlab 2012, Ochmian et al. 2013].

Determination of proline content. The concentration of free proline was measured three times in each blueberry leaf, and proline accumulation was determined according to Bates et al. [1973].

Identification of phenolic compounds. Polyphenolic compounds were analyzed using UPLC-PDA--MS/MS Waters ACQUITY system (Waters, Milford, MA, USA) consisting of a binary pump manager, sample manager, column manager, photo diode array (PDA) detector, and tandem quadrupole mass spectrometer (TQD) with electrospray ionization (ESI) [Mijowska et al. 2016].

Identification of mineral contents. The contents of elements in leaves were determined after mineralization: N, P, K, and Ca were determined after wet mineralization in H_2SO_4 (96%, Chempur, Poland) and $HClO_4$ (70%, Chempur, Poland), whereas Cu, Zn, Mn, and Fe were determined after mineralization in HNO_3 (65%) and $HClO_4$ (70%) in the ratio of 3 : 1 [IUNG 1972]. The total N concentration was determined by the Kjeldahl distillation method, and N-NO_3 and N-NH_4 was determined potentiometrically [Lityński et al. 1976]. The K content was measured using atomic emission spectrometry, whereas the content of Mg, Ca, Cu, Zn, Mn, and Fe was measured using flame atomic absorption spectroscopy. The P content was assessed by the colorimetric method.

Statistical analysis

All statistical analyses were performed using Statistica 12.5 (StatSoft Polska, Cracow, Poland). Non-parametric methods (Kruskal–Wallis test) were used if neither the homogeneity of variance nor the normality of distribution was established previously. Statistical significance of the differences between means was determined by testing the homogeneity of variance and normality of distribution, followed by multifactor ANOVA with the Tukey's post hoc test. The significance was set at $p < 0.05$.

RESULTS AND DISCUSSION

Plant growth

In our experiment, white and violet LED light and white fluorescent light had a positive effect on the growth of blueberry plants, whereas red fluorescent light did not have the predicted effect on plant growth. Although the light spectrum of red fluorescent lamps (λ 600–700 nm) is supposed to increase photosynthetic activity, plant growth was not observed in either

blueberry cultivar since the beginning of the experiment. Moreover, doubling the number of fluorescent lamps in order to increase the luminous flux did not have a positive effect on plant growth efficiency. Plant growth may have been negatively affected by the low photosynthetic photon flux density of these lamps. They also emit wavelengths in the very limited 600–700 nm range. Studies have shown that blue light has a significant effect on chlorophyll biosynthesis [Kamiya et al. 1981, Shin et al. 2008, Klamkowski et al. 2012]. It was found that the low concentrations of Chl *a* and *b*, which in plants have been treated with monochromatic red light, have even led to photooxidative stress in plants due to an increase of O_2^- and H_2O_2. radicals [Bae and Choi 2008, Hogewoning et al. 2010]. A minimum of 20−30 µmol s^{-1} m^{-2} of blue light is necessary to reach natural-like growth and plant morphologies [Barnes and Bugbee 1992]. Other experience shows that the most effective lighting is red and blue in the correct ratio for the species [Ohtake et al. 2018, Pennisi et al. 2019, Chiang et al. 2020]. Therefore, we decided to stop the experiments with red fluorescent light. The plants did not develop new shoots, leaves, or root systems, and they started to dry out. The leaves were green and firm, but gradually turned brown and dried up. On the other hand, the blueberry plants illuminated with the other three light types (white fluorescent, white LED, and violet LED) showed undisturbed growth. The plants looked typical, had a vivid green color, and similar internode lengths. Under phytotron conditions, we found that plants of the Aurora cultivar were 7.5% higher than the plants of Huron cultivar regardless of the light source (Tab. 1). However, the analysis of the type of light showed that violet LED light had the worst impact on plant growth. Despite having a similar photosynthetically active radiation (PAR) value, the plants of both cultivars had the lowest height compared to the fluorescent and LED white light (Tab. 1, Fig. 2).

Table 1. Characteristics of the highbush blueberry 'Aurora' and 'Huron' depending on the type of light

Plant parameters		Cultivars	Type of light			
			fluorescent white lamp	white LED	violet LED	mean
Height of plants (cm)		Aurora	25.8 ±1.7d	24.1 ±1.2c	20.5 ±1.9a	23.5B
		Huron	22.9 ±1.3b	22.0 ±1.5b	20.6 ±1.6a	21.8A
		mean	24.4B	23.1B	20.6A	
Leaf area (cm^2)		Aurora	6.62 ±0.42ab	7.63 ±0.49b	7.15 ±0.39ab	7.13A
		Huron	7.12 ±0.39ab	6.95 ±0.44ab	6.11 ±0.35a	6.73A
		mean	6.87AB	7.29B	6.63A	
Proline (µmol g^{-1})		Aurora	4.67 ±0.17a	5.85 ±0.22b	8.11 ±0.27d	6.21A
		Huron	7.23 ±0.24cd	6.71 ±0.29c	9.06 ±0.25e	7.67B
		mean	5.95A	6.28A	8.59B	
Colours parameters CIE	*L**	Aurora	46.49 ±3.17d	42.59 ±2.58bc	41.28 ±3.37b	43.45B
		Huron	39.96 ±1.97a	39.69 ±1.84a	43.06 ±2.99c	40.90A
		mean	43.23A	41.14A	42.17A	
	*a**	Aurora	–32.29 ±1.73bc	–33.03 ±1.45c	–29.58 ±1.33a	-31.63A
		Huron	–29.14 ±1.40a	–31.85 ±0.99b	–28.51 ±1.17a	-29.83A
		mean	–30.72AB	–32.44B	–29.05A	
	*b**	Aurora	24.42 ±1.82d	21.4 ±0.98c	18.16 ±1.06a	21.33A
		Huron	20.83 ±1.38bc	20.89 ±1.15bc	20.11 ±1.30b	20.61A
		mean	22.63B	21.15B	19.14A	

Mean values denoted by the same letter do not differ statistically significantly at 0.05 according to the Tukey's test. Small letters indicate the interaction between factors (cultivars and light), large letters indicate the main factors

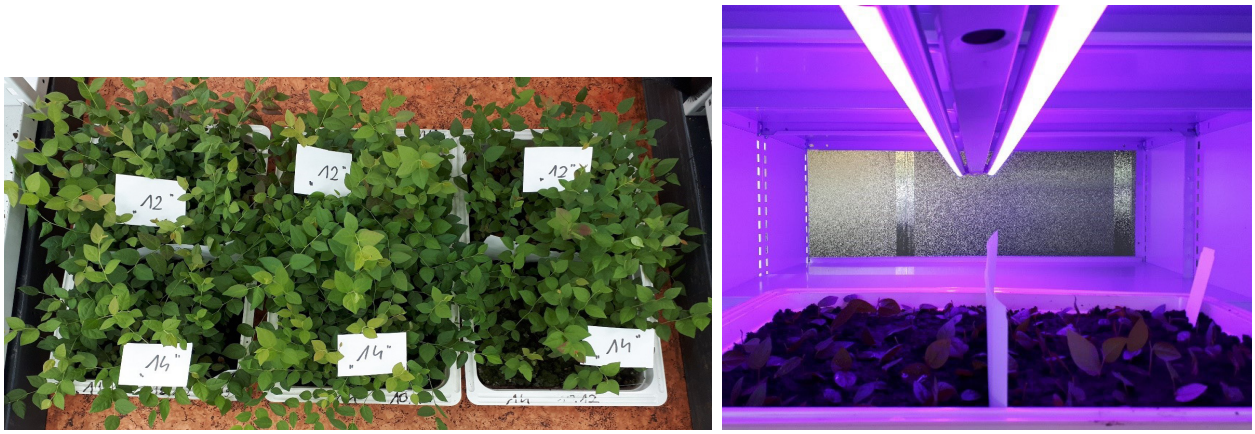

Fig. 2. Plants of the highbush blueberry 'Aurora' and 'Huron' depending on the light used; from the left – white LED, white fluorescent lamps, violet LED

Analysis of the light types showed that the plants had the largest area of one leaf (7.29 cm^2) under white LED light and the smallest one under violet LED light (6.63 cm^2) (Tab. 1). Plants of both cultivars illuminated with violet LED light were also less green – it is indicated by a^* and b^* parameters. This suggests that the plants illuminated with this light had less amount of chlorophyll. The leaves of the Aurora cultivar were lighter than those of Huron, as evidenced by the CIE parameters L^* (Tab. 1). The brightest leaves of Aurora cultivar were measured on plants that were illuminated with a fluorescent white lamp. The value of the L^* parameter (reaching from 0 to 100, black to white, respectively) is usually used for tracking color changes [Ochmian et al. 2019a]. The leaf color determined by the CIE L^* parameter was typical for highbush blueberry and similar to that of plants in other studies [Ochmian 2012].

According to several authors [Yang and Zhang 2011, Krupa-Małkiewicz et al. 2019], elevated proline levels in plant tissues are fairly good indicators of the negative effects of various stress factors on plants. In the present study, 23.5% higher proline level was observed in 'Huron' plants than in 'Aurora' plants. This may indicate that compared to 'Huron' plants, 'Aurora' plants have higher sensitivity to light stress. Moreover, higher proline values were observed in plants of both cultivars growing under the influence of violet LED light (Tab. 1). Similar results were described by Chen et al. [2012] in the highbush blueberry cultivar Sharpblue, which had a higher resistance to elevated temperatures but also a higher proline content than the other 3 cultivars – Duke, Brigitta, and Misty.

Macro- and microelements

Compared to the other light sources, the violet LED has increased the accumulation of N, K, and Ca in the 'Aurora' leaves and the opposite reaction of N and Mg uptake was observed in 'Huron' (Tab. 2). Depending on the standards for highbush blueberry developed by different authors [Eck 1988, Bal 1997, Komosa 2007, Ochmian et al. 2021], most of the investigated macroelements in the leaves were at an optimal level. The exception was calcium; although it was at a high level in the substrate 38.9 mg 100 g^{-1}, optimum 10–30 mg 100 g^{-1} (Tab. 2), we found that it was significantly below the recommendations for blueberry leaves; 0.40–0.80 mg 100 g^{-1}. The content of macroelements in the leaves of both cultivars was similar to that in the leaves of plants grown in peat under field conditions [Ochmian et al. 2019a]. However, in field conditions (loamy sand), low nitrogen content was recorded in the leaves even after the application of the optimal doses of nitrogen [Ochmian et al. 2018]. The nutrient content in the leaves is a good indicator of plant nutritional status. However, in the case of blueberry bushes, this can be difficult to determine because different authors had different specifications of the optimal abundance of certain elements (for example N) in blueberry leaves 1.7%–2.1% [Hanson 2006], 2.10% [Smolarz and

Table 2. The content of macroelements and microelements in leaves of highbush blueberry 'Aurora' and 'Huron' depending on the type of light

Mineral element	Cultivars	Type of light			
		fluorescent white lamp	white LED	violet LED	mean
		g 100 g^{-1}			
N	Aurora	1.78 ±0.06*a*	1.89 ±0.05ab	1.95 ±0.07b	1.87A
	Huron	2.24 ±0.0.07c	2.35 ±0.08c	1.97 ±0.06b	2.19B
	mean	2.01A	2.12A	1.96A	
P	Aurora	0.23 ±0.01a	0.25 ±0.01ab	0.22 ±0.00a	0.23A
	Huron	0.29 ±0.01c	0.28 ±0.01bc	0.31 ±0.01c	0.29A
	mean	0.26A	0.27A	0.27A	
K	Aurora	0.41 ±0.02b	0.37 ±0.01a	0.46 ±0.02c	0.41A
	Huron	0.50 ±0.02cd	0.52 ±0.02de	0.56 ±0.02e	0.53B
	mean	0.46A	0.45A	0.51A	
Ca	Aurora	0.23 ±0.00a	0.24 ±0.01ab	0.27 ±0.01bc	0.25A
	Huron	0.28 ±0.01c	0.26 ±0.01ac	0.29 ±0.01c	0.28A
	mean	0.26A	0.25A	0.28A	
Mg	Aurora	0.15 ±0.01a	0.17 ±0.01ac	0.16 ±0.01ab	0.16A
	Huron	0.18 ±0.01bc	0.19 ±0.01c	0.15 ±0.01a	0.17A
	mean	0.17A	0.18A	0.16A	
		mg 1000 g^{-1}			
Fe	Aurora	47.3 ±2.7a	53.2 ±3.4ab	58.9 ±3.2b	53.1A
	Huron	84.4 ±5.4e	67.8 ±4.3c	77.5 ±4.9d	76.6B
	mean	65.8AB	60.5A	68.2B	
Zn	Aurora	5.23 ±0.19a	5.74 ±0.23b	7.05 ±0.28c	6.01A
	Huron	7.11 ±0.21c	7.85 ±0.24d	8.36 ±0.20e	7.77B
	mean	6.17A	6.80B	7.71C	
Mn	Aurora	72.1 ±0.3ab	65.8 ±0.2a	83.4 ±0.2c	73.8A
	Huron	94.2 ±0.4d	99.4 ±0.3d	80.6 ±0.3bc	91.4B
	mean	83.2A	82.6A	82.0A	
Cu	Aurora	1.77 ±0.04bc	1.82 ±0.05c	1.64 ±0.03a	1.74A
	Huron	1.73 ±0.03b	1.94 ±0.04d	1.79 ±0.03bc	1.82A
	mean	1.75A	1.88B	1.72A	

Explanations in Tab. 1

Mercik 1993], 1.52%–2.17% [Glonek and Komosa 2006], 1.8–2.1% [Eck 1988], 2.25%–2.75% [Pliszka 2002], 1.8%–2.0% [Sagoo et al. 2016].

The nitrogen content in the leaves of the 'Aurora' and 'Huron' plants had 1.87 and 2.19 mg 100 g^{-1}, respectively (Tab. 2). The high nitrogen content in the leaves of the 'Huron' plants grown under white LED light was also confirmed by their intensive color (Tab. 1). The type of light also influenced the iron content in the leaves of the two cultivars. The average iron content in the plants exposed to violet LED light was 11.3% higher than in plants exposed to white LED light. 'Huron' plants had on average 30.7% more iron than 'Aurora' plants (Tab. 2). Despite the lower amount of Fe in the leaves of 'Aurora' shrubs than that in the recommendations by Eck [1988], the plants did not show any external signs of Fe deficiency. Similar to N, the standards for Fe content differ among studies by different authors (43–61 mg 1000 g^{-1} in Glonek and Komosa 2006; 60–200 mg 1000 g^{-1} in Eck 1988]. In both cultivars, Zn and Cu contents were lower than those in the standards (respectively; optimum 8–30 mg 1000 g^{-1} and 2–20 mg 1000 g^{-1}), and low copper content in peat soils is common [Ochmian et al. 2019a]. However, in other field experiments, the iron content in the leaves was at a higher level [Ochmian et al. 2019b] compared to the plants grown in a phytotron. Glonek and Komosa [2006] found similar Fe content in blueberry leaves (53.9–57.7 mg kg) as those in the leaves of 'Aurora', and higher Mn content (107.6–128.0 mg kg) than those in the leaves of both cultivars from the present study. Mn is an essential element that is bound to a number of essential enzymes; for example, the activity of superoxide dismutase is suppressed by low Mn status [Li and Zhou 2011]. The optimum Mn content in leaves should be 0–350 mg 1000 g^{-1} [Eck 1988]. Rivera et al. [2015] concluded that the Fe content of the soil depends on how it is used.

Polyphenols

Studies [Oszmiański et al. 2011, Li et al. 2013, Değirmencioğlu et. al. 2017] have shown that highbush blueberry leaves are a valuable source of polyphenols. In the leaves of the two investigated blueberry cultivars, we identified 12 phenolic acids, eight flavonols, and six flavan-3-ols. High polyphenol content may indicate the effect of a stress factor, in this case a light source (namely the range of light wavelengths). Flavonoids (including flavonols, anthocyanins) and carotenoids play a major role in protecting plants against the harmful effects of short-wave super-violet light (UV 280–400 nm) [Pilarski and Kocurek 2014, Vidović et al. 2015, Ochmian et al. 2019b]. The observed high content of different polyphenols in blueberry leaves depended mainly on the type of light, but also on the cultivar. Plants illuminated with violet LED light had the highest polyphenol content; they were also the lowest and had the smallest leaves. This may explain the increased accumulation of Fe and Zn in leaves treated with violet light. These elements are important for the activity of the enzymes, catalase (Fe) and superoxide dismutase (Fe, Zn) [Bhoomika et al. 2013]. This suggested that this type of light was a stress factor for blueberry plants. Plants illuminated with white fluorescent light had the lowest level of polyphenols in their leaves; in addition, they were the tallest and had the largest leaves. There was also a significant difference in polyphenol content between the cultivars. The average content of the determined polyphenols in 'Aurora' was 6705.27 mg 100 g^{-1}, and it was 34.5% higher than that in 'Huron' (Tab. 3). The polyphenol content in the leaves of 'Aurora' was similar to that in the leaves of *Vaccinium myrtillus* [Değirmencioğlu et al. 2017]. Li et al. [2013] and Oszmiański et al. [2011] indicated that the leaves of highbush blueberry are richer in polyphenols compared to the leaves of other fruit plants, including blackberry, raspberry, honeyberry, and strawberry.

A positive relationship was observed between the content of two main groups of polyphenols, phenolic acids and flavonols, in plants grown under violet LED light. The content of these polyphenols was very high in these plants. On average, the results for both cultivars (Tab. 3) showed that compared to white fluorescent light and white LED light, violet LED light caused an increase in leaf polyphenols by as much as 29% and 23%, respectively. Additionally, plants illuminated with violet LED light had high proline content, which led us to conclude that violet light caused stress in the examined plants. The highest total polyphenol content (7440.44 mg 100 g^{-1}) was recorded in Aurora cultivars illuminated with violet LED light, whereas the lowest was recorded in Huron cultivars illuminated with white fluorescent light (54.5% lower than that in

Table 3. The content of polyphenols in leaves of highbush blueberry 'Aurora' and 'Huron' depending on the type of light

Cultivars	Aurora			Huron			Aurora	Huron
Type of light	fluorescent white lamp	white LED	violet LED	fluorescent white lamp	white LED	violet LED	mean	mean
1	2	3	4	5	6	7	8	9
Compounds (mg 100 g^{-1} DW)	Phenolic acid							
1-*O*-Caffeoylquinic acid	30.89 ±0.06e[a]	10.19 ±0.02b	11.65 ±0.02c	14.23 ±0.03d	8.26 ±0.02a	9.91 ±0.02b	17.58B	10.80A
trans-3-*O*-Caffeoylquinic acid	538.37 ±1.08c	476.26 ±0.95b	1030.20 ±2.06e	327.89 ±0.66a	480.60 ±0.96b	933.40 ±1.87d	681.61B	580.63A
cis-3-*O*-Caffeoylquinic acid	17.06 ±0.03e	7.86 ±0.02b	14.53 ±0.03d	10.46 ±0.02c	10.64 ±0.02c	5.49 ±0.01a	13.15B	8.86A
3-*O*-*p*-Coumaroylquinic acid	72.46 ±0.11d	23.82 ±0.05b	40.39 ±0.08c	8.76 ±0.02a	11.50 ±0.02a	206.36 ±0.41e	45.56A	75.54B
5-*O*-*p*-Coumaroylquinic acid	2704.32 ±4.33d	2624.76 ±5.25d	2964.60 ±5.93e	894.97 ±1.79a	1072.78 ±2.15b	1483.00 ±2.97c	2764.56B	1150.25A
trans-5-*O*-Caffeoylquinic acid	20.01 ±0.04b	13.16 ±0.03a	23.55 ±0.05c	22.69 ±0.05c	28.04 ±0.06d	27.90 ±0.06d	18.91A	26.21B
5-*O*-Caffeoylquinic acid	269.52 ±0.53b	372.83 ±0.75d	688.64 ±1.38f	183.31 ±0.37a	328.33 ±0.66c	529.83 ±1.06e	443.66B	347.16A
4-*O*-Caffeoylquinic acid	31.72 ±0.06d	7.44 ±0.01c	5.42 ±0.01b	4.91 ±0.01b	4.94 ±0.01b	2.19 ±0.00a	14.86B	4.01A
3-*p*-coumaroyl-5-feruloy-lquinic	18.1 ±0.04f	0.39 ±0.00a	1.32 ±0.00b	9.52 ±0.02e	2.15 ±0.00c	3.03 ±0.01d	6.60B	4.90A
3,5-Di-*O*-caffeoylquinic acid	6.28 ±0.01a	41.88 ±0.08e	21.21 ±0.04d	7.28 ±0.01b	9.62 ±0.02c	65.15 ±0.13f	23.12A	27.35B
4,5-Di-*O*-caffeoylquinic acid	6.28 ±0.01a	7.01 ±0.01b	8.12 ±0.02c	8.76 ±0.02d	15.24 ±0.03f	13.89 ±0.03e	7.14A	12.63B
cis-5-*O*-*p*-Coumaroylquinic acid	3.65 ±0.01b	3.98 ±0.01b	6.25 ±0.01c	3.59 ±0.01b	2.81 ±0.01a	2.51 ±0.01a	4.63B	2.97A
Total	3718.66 ±7.65d	3589.58 ±7.18d	4815.89 ±9.63e	1496.37 ±2.99a	1974.92 ±3.95b	3282.66 ±6.57c	4041.37B	2251.31A
	Flavonols							
Myricetin 3-*O*-galactoside	13.09 ±0.03c	16.58 ±0.03d	31.89 ±0.06e	1.83 ±0.00a	6.71 ±0.01b	13.35 ±0.03c	20.52B	7.30A
Myricetin 3-*O*-glucoside	8.10 ±0.02d	0.68 ±0.00bc	0.97 ±0.00c	0.11 ±0.00a	0.30 ±0.00ab	0.64 ±0.00bc	3.25B	0.35A
Myricetin hexoside-acetate	1.19 ±0.00b	0.92 ±0.00b	2.34 ±0.00d	0.40 ±0.00a	1.55 ±0.00c	2.39 ±0.00d	1.48A	1.45A
Quercetin 3-*O*-diglucoside	0.33 ±0.00a	0.37 ±0.00a	1.92 ±0.00c	0.41 ±0.00a	0.64 ±0.00b	3.21 ±0.01d	0.87A	1.42B
Quercetin 3-*O*-rutinoside	26.59 ±0.05c	29.14 ±0.06d	82.59 ±0.17	14.99 ±0.03a	19.17 ±0.04b	34.98 ±0.07e	46.11B	23.05A
Quercetin 3-*O*-rutinoside	1.81 ±0.00c	1.77 ±0.00c	5.55 ±0.01d	0.25 ±0.00a	1.05 ±0.00b	0.95 ±0.00b	3.04B	0.75A

Table 3 cont.

1	2	3	4	5	6	7	8	9
Quercetin 3-*O*-galactoside	5.45 ±0.01b	4.83 ±0.01a	14.33 ±0.03e	8.81 ±0.02c	9.89 ±0.02d	35.88 ±0.07f	8.20A	18.19B
Quercetin 3-*O*-glucoside	15.22 ±0.03a	15.83 ±0.03a	45.18 ±0.09c	14.76 ±0.03a	22.99 ±0.05b	47.89 ±0.10c	25.41A	28.55A
Quercetin 3-*O*-(6"-malonyl) glucoside	1.69 ±0.00a	1.34 ±0.00a	5.07 ±0.01d	2.31 ±0.00b	3.23 ±0.01c	8.68 ±0.02e	2.70A	4.74B
Quercetin 3-*O*-(6"-cetyl) galactoside	1.09 ±0.00a	1.14 ±0.00a	3.46 ±0.01c	2.41 ±0.00b	3.21 ±0.01c	4.13 ±0.01d	1.90A	3.25B
Quercetin 3-*O*-arabioside	1.38 ±0.00c	1.12 ±0.00bc	3.04 ±0.01d	0.68 ±0.00a	0.91 ±0.00b	0.62 ±0.00a	1.85B	0.74A
Isorhamnetin 3-*O*-rutinoside	0.66 ±0.00a	0.85 ±0.00a	26.48 ±0.05e	1.48 ±0.00b	1.82 ±0.00c	6.72 ±0.01d	9.33B	3.34A
Kaempferol 3-*O*-glucoside	2.36 ±0.00c	1.85 ±0.00b	9.97 ±0.02d	1.26 ±0.00a	1.53 ±0.00ab	1.83 ±0.00b	4.73B	1.54A
Isorhamnetin3-*O*-rhamnosyl-hexoside	248.87 ±0.5e	223.40 ±0.45d	7.83 ±0.02c	5.13 ±0.01b	3.19 ±0.01a	7.98 ±0.02c	160.03B	5.43A
Syringetin 3-*O*-galactoside	28.49 ±0.06d	3.65 ±0.01c	93.50 ±0.19e	0.79 ±0.00a	0.82 ±0.00a	2.71 ±0.01b	41.88B	1.44A
Myricetin rhamnosyl-hexoside	6.66 ±0.01d	13.17 ±0.03e	2.12 ±0.00c	0.84 ±0.00a	0.73 ±0.00a	1.55 ±0.00b	7.32B	1.04A
Myricetin dihexoside-acetate	5.11 ±0.01c	0.53 ±0.00a	27.03 ±0.05d	0.54 ±0.00a	0.41 ±0.00a	2.87 ±0.01b	10.89B	1.27A
Quercetin rhamnosyl-hexoside	3.24 ±0.01b	5.99 ±0.01c	166.93 ±0.33d	2.00 ±0.00a	3.83 ±0.01b	5.84 ±0.01c	58.72B	3.89A
Total	371.33 ±0.73e	323.18 ±0.65d	530.20 ±3.85f	59.00 ±0.12a	81.98 ±0.16b	182.21 ±0.36c	408.23B	107.73A
				Flavan-3-ols				
(+)-Catechin	33.12 ±0.07d	29.61 ±0.06c	26.48 ±0.05c	38.05 ±0.08e	14.68 ±0.03b	11.25 ±0.02a	29.74B	21.33A
Procyanidin tetramer	11.12 ±0.02c	9.89 ±0.02b	9.97 ±0.02b	5.75 ±0.01a	9.26 ±0.02b	4.87 ±0.01a	10.33B	6.63A
(-)-Epicatechin	7.59 ±0.02d	9.51 ±0.02e	7.83 ±0.02d	3.39 ±0.01a	4.64 ±0.01b	5.68 ±0.01c	8.31B	4.57A
Procyanidin dimer	44.61 ±0.09b	51.34 ±0.10b	93.50 ±0.19c	132.97 ±0.27d	197.50 ±0.4e	12.53 ±0.03a	63.15A	114.33B
Procyanidin tetramer	10.60 ±0.02c	4.67 ±0.01b	2.12 ±0.00a	27.33 ±0.05d	4.62 ±0.01b	9.49 ±0.02c	5.80A	13.81B
Procyanidin trimer	312.98 ±0.63f	37.49 ±0.07b	27.03 ±0.05a	72.70 ±0.15c	78.94 ±0.16d	162.12 ±0.32e	125.83A	104.59B
Total	420.02 ±0.71e	142.49 ±0.28a	166.93 ±0.33a	280.19 ±0.56c	309.64 ±0.62d	205.94 ±0.41b	243.15A	265.26B
Polymeric procyanidin	2079.6 ±4.2e	2032.5 ±4.1de	1927.4 ±3.9c	1549.1 ±3.1a	1971.3 ±3.9cd	1784.9 ±3.6b	2013.2B	1768.4A
Degree of polymerization	7.15b	6.83a	7.10ab	10.84e	8.76d	7.67c	7.03A	9.09B
Total of polyphenols	6589.6 ±12.0D	6087.8 ±10.D	7440.4 ±14.4E	3384.6 ±6.7A	4337.8 ±7.1B	5455.7 ±8.6C	6705.3B	4392.7A

Explanations in Tab. 1

'Aurora'). Very high contents of trans-3-*O*-caffeoylquinic acid (1030.20 mg 100 g^{-1}) and 5-*O*-p-coumaroylquinic acid (2964.60 mg 100 g^{-1}) were also recorded in Aurora cultivars grown under violet LED light. Generally, among the 35 examined polyphenols, 5-*O*-p-coumaroylquinic acid occurred in the highest amount in the investigated plants. Degree of polymerization is an important structural feature determining the bitterness and astringency of taste and the biological activity of proanthocyanidins [Waterhouse and Ebeler 1998]. Thus, in measured samples were noted the statistical differences between fluorescent white lamp and LED (white and violet). The highest DP was found in the sample after fluorescent white lamp used and was 17% higher than in the sample after LED.

Production economics

When choosing a particular light source, manufacturers are primarily guided by economic profit. They expect a good quality product that is also energy-efficient at a low price. Violet LED lamps used in this experiment were more expensive than white LED lamps and white fluorescent lamps. In economic calculations (Tab. 4), we noticed the scale of savings that can be achieved with LEDs solution. The phytotron, in which we have conducted the experiment, allows us to produce 20.000 plantlets in one cycle. This requires 200 fluorescent lamps with a length of about 120 cm. In the present study, a white fluorescent lamp was 76.26% cheaper than a violet LED lamp and 44.51% cheaper than a white LED lamp. Taking into account the purchase price of fluorescent lamps, the price of electricity, energy consumption, photoperiods, bulb life, and the annual cost of bulb maintenance, we calculated the annual cost of phytotron maintenance (Tab. 4). Considering all costs generated in the annual cycle in our phytotron, we found that the cheapest solution were white LED lights (3044 euros a piece). Despite the high price for a single violet LED lamp, the cost of maintaining the phytotron was slightly higher (3305.60 euros). This was because of the longer service life of fluorescent lamps, which by the manufacturer is 50.000 h. White fluorescent lamps were the most expensive to maintain. Despite the low price of this light source, because of its very short service life (15.000 h), its maintenance cost was 6.555 euros. However, according to the manufacturer, the photosynthetic efficiency of these fluorescent lamps decreases remarkably after 12.000 h. In practice, after 2 years, the fluorescent lamps in phytotrons are usually replaced even if they are still working.

By choosing LED lamps, we achieved about 50% savings compared to using fluorescent lamps. Production economics showed that it is better to use LED sources than other light sources for plant production in phytotrons. Fluorescent lamps are economically disadvantageous, and the mercury contained in them is also dangerous for the environment. LEDs are safe

Table 4. Economic effects of the annual greenhouse maintenance depending on the type of light

Cost of using lamp	Type of light		
	fluorescent white lamp	white LED	violet LED
Price of 1 lamp (EUR)	8.84	3.78	15.93
Electricity consumption (W)	36	18	18
Uptime (h)	15 000	40 000	50 000
Uptime in years	2.57	6.85	8.56
Annual power consumption 1 lamp (16 h/day × 365 days = year × lamp power kW) = kW/year	210	105	105
Price 1 kWh (EUR)	0.14	0.14	0.14
Power consumption cost for 1 lamp per year (EUR)	29.34	14.67	14.67
Annual cost of using 1 lamp (EUR) energy + lamp price	32.78	15.22	16.53
Annual cost of phytotron work (EUR)	6555.29	3044.00	3305.60

for the user and the environment because they are not made of brittle glass, do not heat up, and do not contain any dangerous materials such as mercury [Olle and Viršile 2013].

The results of research on production economics showed that the use of a white LED light source is a good solution for blueberry production. Its maintenance was significantly cheaper than fluorescent lamps, and plants grown under this light source had the largest leaf surface area among all investigated light sources. In addition, on average, the plants grown under white LEDs were vivid green and did not differ in height from the plants grown under white fluorescent light. However, according to the results of our experiment, in order to obtain polyphenol-rich plants for commercial purposes, we recommend the use of violet LED light sources (Tab. 3). The leaves of plants grown under this light source could be used as infusions to provide antioxidant substances. In their *in vitro* studies, Piljac-Žegarac et al. [2009] confirmed that blueberry leaf-based tea is a very good source of strong antioxidants.

CONCLUSIONS

Regardless of the type of light used in the phytotron, the plants of the Aurora cultivar were higher, and they had lighter leaves with higher polyphenol contents and lower proline contents compared to those of the Huron cultivar. When grown under violet LED lights, the plants of both cultivars were lower and had smaller leaves. This light source is a stress factor for the plants, which was evidenced by low CIE *a** and *b** leaf color as well as high contents of total proline and polyphenols. The plants grown under fluorescent white light had a 22.7% lower total of polyphenols, and the plants grown under LED white light had a 19.2% lower total than those grown under violet LED light. In large-scale production of highbush blueberry plants, it is advisable to use white LED light owing to the high quality of the plants grown under this light as well as their beneficial effect on production economics.

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CONFLICT OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

AUTHOR CONTRIBUTION

Conceptualization: M.F-K. I.O., M.K-M. S.L., Material: M.F-K. Methodology: M.F-K. I.O., M.K-M. S.L. Formal analysis and investigation: M.F-K. I.O., M.K-M. S.L. Writing – original draft preparation: M.F-K. I.O., M.K-M. S.L. Writing – review and editing: M.F-K. I.O., Funding acquisition: I.O. Supervision: I.O.

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